

THE BIOLOGICAL BULLETIN

PUBLISHED BY THE MARINE BIOLOGICAL LABORATORY

TUBE-BUILDING AND FEEDING IN THE CHAETOPTERID POLYCHAETE, *SPIOCHAETOPTERUS OCULATUS*

ROBERT D. BARNES

Department of Biology, Gettysburg College, Gettysburg, Pennsylvania

Chaetopterus variopedatus is one of the best known polychaete annelids. The construction of the familiar U-shaped tube of this worm was first studied by Enders in 1908. Enders in a later paper (1909) made some observations on feeding in *Chaetopterus* but failed to recognize the use of the mucous bag. Complete understanding of the feeding mechanism in *Chaetopterus* was provided by the studies of MacGinitie in 1939. Much less is known about the behavior and physiology of other chaetopterid genera. Only a few casual observations of the North Pacific *Mesochaetopterus rickettsii* and *Phyllochaetopterus prolifera* have been reported (MacGinitie and MacGinitie, 1949).

The purpose of this study was to investigate the mechanism of tube-building and feeding in *Spiochaetopterus*, a chaetopterid genus which is rather more typical of the family than is *Chaetopterus*. The species studied was *Spiochaetopterus oculatus* Webster, a very common member of the genus along the North Atlantic coast.

This investigation was carried out at the Duke University Marine Laboratory at Beaufort, North Carolina, during the summer of 1963, and was supported by a National Science Foundation Summer Study Grant. The author wishes to express his appreciation to the Duke University Marine Laboratory for the facilities extended to him during the course of this study. Acknowledgment is also due to Dr. Marion Pettibone of the United States National Museum for her kind assistance and suggestions.

MATERIALS AND METHODS

Worms were collected within the tube, care being taken to dig out the entire tube from the substratum. In studying tube construction, specimens were restricted to a short section of the natural tube, the other part having been cut away. The section containing the worm was then placed in the upper part of a piece of glass tubing having a bore of 1.5 mm. Worms were also entirely removed from their own tube and placed within glass capillary tubes. Transfer was brought about by placing the tube of the worm within the end of a capillary tube (0.8-

1.2 mm. in diameter) which just exceeded the diameter of the worm tube. A dissecting needle was then rolled down the length of the worm's tube, driving the worm out and into the capillary tube. Since removal of the worm caused some damage to the end of the body just in front of the dissecting needle, care was taken to always drive the worm forward. Thus, any damaged segments would be at the posterior end of the body.

The glass tubes containing worms were kept in a vertical position by placing them in a glass cylinder, where they were held against the inner side of the cylinder wall with a large plug of glass wool wrapped in a piece of black cloth. The black cloth provided a good background for visual observations. A short piece of glass tubing having a diameter of 2 cm. was extended through the center of the plug of glass wool to provide for circulation of water in the lower part of the cylinder. The entire cylinder, except during periods of observations, was then submerged in a battery jar of running sea water.

The worms were observed in a vertical position through the glass wall of the cylinder. Observations were made with a binocular dissecting microscope (from which the base had been removed) suspended horizontally by the arm from a clamp attached to a ring stand.

RESULTS AND OBSERVATIONS

Spiochaetopterus oculatus is a small tube-inhabiting chaetopterid polychaete, varying in length from 3.0 to 6.0 cm. Like many other members of the family Chaetopteridae, the body is divided into three regions. The broad anterior region (Fig. 1, A) is composed of a poorly defined head followed by nine segments. The parapodia of these segments are limited to a short notopodium, each of which is provided with a fan of capillary setae. The fourth notopodium is peculiar in possessing a giant blade-like seta in addition to the capillary bundle.

The cylindrical middle region of the body (Fig. 1, C) is composed of 18 to 37 segments, although 21 to 24 segments are most commonly present. Each of these segments is provided with distinctive parapodia composed of a foliaceous notopodium and an uncinata neuropodium. The foliaceous notopodium will be described in detail later.

The terminal body region is made up of a large but varying number of segments. It is somewhat similar to the middle region of the body except that the notopodia, rather than being foliaceous, are reduced to antenna-like processes (Fig. 1, D).

The tube

The tube of *Spiochaetopterus* is a vertical annulated structure composed entirely of a secreted cornified, or chitin-like, material. The tube is built vertically in the substratum with from 2 to 10 mm. of its length projecting above the surface. The total length of the tube varies greatly, and this variation is perhaps related to the nature of the substratum. At Beaufort, North Carolina, *Spiochaetopterus* is most abundant in a muddy substratum, where it occurs from below the low-tide mark through the lower third of the intertidal zone. In such habitats the worm may have a density as great as 25 to 35 individuals per square foot. In sandy

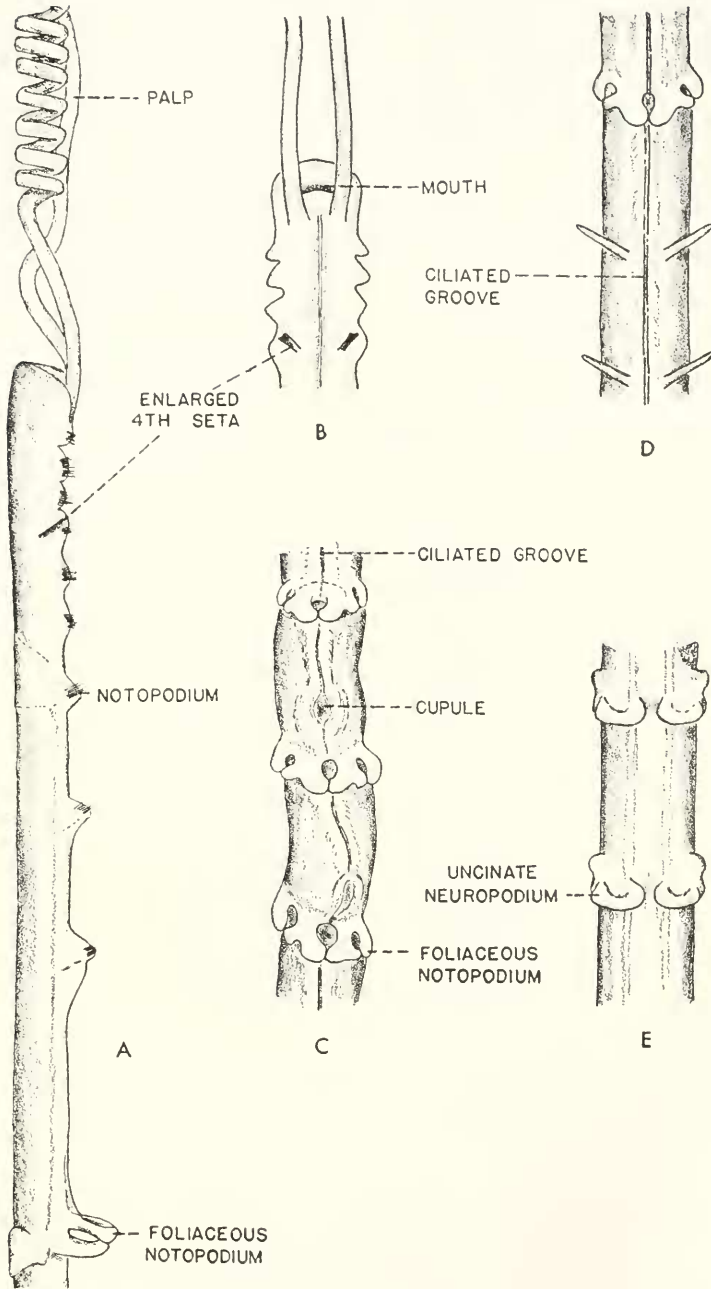


FIGURE 1. External structure of *Spiochaetopterus oculatus*. A. Lateral view of anterior body region and first foliaceous notopodium of middle body region. B. Dorsal view of anterior end of body. C. Dorsal view of three segments of middle body region. D. Dorsal view of last segment of middle body region and first two segments of posterior body region. E. Ventral view of two segments of middle body region showing uncinete neuropodia.

substrata the species is much less abundant and careful searching may be necessary to locate the tubes.

In several muddy habitats in the Newport River Estuary, from which specimens were regularly collected, the total length of the tube mostly ranged from 8.0 to 12.0 cm. However, on sand flats tubes were obtained which reached a length of more than 50 cm.

The diameter of the tube is not nearly so variable as its length. The internal diameter is generally about 0.7 mm., although one had an internal diameter of 1.2 mm. The wall is thickest, about 0.03 mm., in the upper extent of the tube.

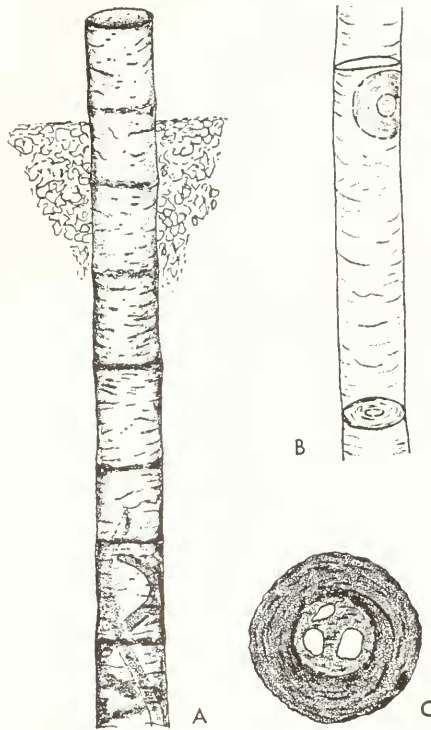


FIGURE 2. Tube structure. A. Upper end of tube showing relationship of opening to substratum. B. A short section of the lower region of the tube showing an old partition (top) plastered against the wall of the tube and a functional partition (bottom) in place. C. Surface view of a partition. Note thinner central area perforated by three openings.

The tube in this region (Fig. 2, A) is tough, rigid, markedly annulated, and opaque to blackish in color. The annulations are formed by a slightly thicker area of tube wall and are spaced 1.0 to 1.5 mm. apart.

Since the oldest part of the tube is generally the upper portion, the tube wall tends to become thinner as it extends downward into the substratum. The lower part of the tube is colorless and transparent, with no noticeable annulations and with thin, easily collapsible walls.

At some point near the bottom of the tube, and always within the thin trans-

parent section, the lumen is obstructed by a partition (Fig. 2, B). The partition is shaped somewhat like a button (Fig. 2, C). The peripheral portion is relatively thick and joins with the tube wall. The circular central area is thinner and perforated by one to four openings. The bore of the tube is thus never completely blocked, and the openings in the partition permit continual water circulation. The partitions are periodically removed and new ones constructed at different levels. The old partitions when removed are plastered against the inner side of the tube wall, and can be observed all along the length of the more transparent lower quarter of the tube. The function of the partitions is not certain. They may serve to prevent the thin walls of the lower part of the tube from collapsing.

Mechanism and movement within the tube

Like all chaetopterids, the activities of *Spiochaetopterus* are limited to the confines of its tube. Yet worms observed within glass tubes or within the transparent sections of their own tubes exhibited considerable facility of movement. The body of the worm maintains contact with both sides of the tube wall. On one side of the tube this contact is supplied by the convex ventral surface of the anterior region of the body and by the uncinatæ neuropodia (Fig. 1, E) of the middle and posterior regions of the body. These neuropodia have the form of a pair of slightly curved shelves.

The opposite wall of the tube is contacted by the notopodia of the anterior and middle body regions. The anterior notopodia are slightly tapered processes having a bundle of capillary setae. The notopodia of the middle section are foliaceous and each consists of two parts as shown in Figure 1, C. The foliaceous processes are normally held at right angles to the body so that their distal margins touch the wall of the tube.

The worm may be oriented within the tube with the head directed upward or downward, but most commonly it assumes an upward position. In either position the worm can readily move up or down the length of the tube. Slow upward movement appears to be largely brought about by the leg-like action of the anterior notopodia. These appendages push against the side of the tube, one notopodium acting alternately with the notopodium on the opposite side. The setae bundles are extended and pushed out and downward against the tube wall. Most conspicuous are the 7th, 8th, and 9th notopodia which are the largest notopodia in the anterior part of the body. The action of these notopodia involves not only extension but an outward turning of the anterior margin.

In slow downward movement, the worm appears to release contact with the tube wall and slowly sink.

Rapid movement involves body contraction and is essentially peristaltic in nature. The uncinatæ neuropodia of the middle and posterior body regions appear to provide the principal means of anchorage in this type of movement.

A worm can easily reverse itself within the tube. In changing from a head-up to a head-down position, the anterior end is bent downward and then moves down the tube against the posterior part of the body, which is simultaneously moving upward in the opposite direction. The turning point of the body thus remains more or less at the same level. Reversing from a head-downward position may

be carried out as just described, with the anterior end moving upward through the tube, or the worm may perform a reverse jackknife, in which the posterior end turns downward and moves down the tube.

Tube construction

Secretions for tube construction are produced by epidermal glands which open onto the ventral surface of the anterior region of the body. This secretory surface is large. It extends from near the anterior margin of the head through the entire anterior body region, *i.e.*, to the level of the 9th parapodia, and covers the entire convex ventral side of the body. It is hoped that the histology of the glandular area, as well as other aspects of the histology of *Spiochaetopterus*, will be described in a later paper.

Observations on tube construction were made on worms confined to a very short section of the original tube, the remainder of the tube having been removed. An animal so confined immediately began the construction of additions to the original tube. Such additions were made to either end of the tube but most commonly were initiated at the upper end.

The actual laying down of tube wall is preceded by "exploratory" movements of the anterior end of the body. The anterior end is extended out of the tube as far as the 7th parapodia or a lesser distance and then withdrawn. This movement may be repeated many times with the body often rotating to cover a new arc at each extension. The palps during this time are extended downward between the foliaceous notopodia.

At the time of secretion the anterior end is slowly extended out of the tube, rotating slightly side to side in the process. The projecting anterior end appears markedly turgid with the front margin flared. The body extends out of the tube as far as the 7th parapodia and when this level is reached, the head bends dorsally at right angles to the body. The flexure is located at about the level of the 4th parapodia. At the end of this movement (Fig. 3, A) which may take 10 to 15 seconds, the body is quickly withdrawn, leaving behind and in place a delicate one-half cylinder attached to the older section of the tube. The length of the new addition is equivalent to the distance between the flexure and the level of the body at the mouth of the tube.

The worm now rotates 180° and repeats the secretory projecting movement to lay down another half-cylinder of tube. The second half-cylinder is attached to the first half to form a complete cylindrical addition or section of tube. Such a section would approximate an annulated section in an older part of the tube.

With the completion of the cylinder, the worm now moves up and down applying the ventral secretory surface of the body against the inner surface of the new addition, reinforcing the tube wall with additional secretions. These reinforcing movements may be coupled with exploratory movements, preceding the secretion of another section of tube. Within the period of an hour several new sections may be added to the tube.

Having added to the top end of the tube, the worm may reverse itself and begin additions to the lower end of the tube. Under natural conditions, additions are probably made chiefly to the lower end of the tube.

The reinforcing of the inner wall of the tube with additional secretions is ap-

parently a continual process and would account for the gradual thickening of the tube wall between new and older sections. The convex ventral surface is always pressed against the tube surface.

The transverse partitions which partially block the lower part of the tube are secreted by the head region. The worm reverses itself in the tube if previously directed upward, and then moves downward toward the lower part of the tube. At the level at which the partition is to be placed, the worm halts its downward movement. The head is flexed slightly inward (dorsally) and then rapidly

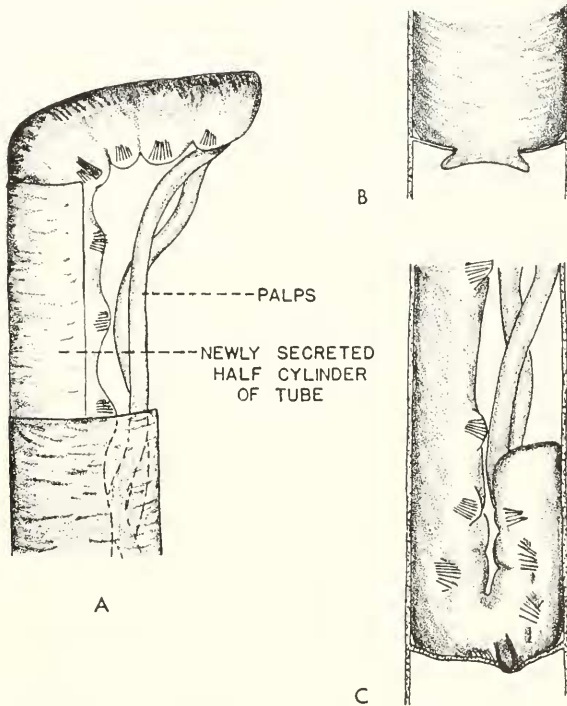


FIGURE 3. Tube construction. A. Worm secreting addition to tube. B. Head of worm secreting first part of a partition. Anterior median region of head is forced through the initially open central area of partition. C. Worm in process of removing a partition by cutting its junction with the tube wall with the heavy blade-like 4th seta.

rotated. It is during this rotation, which lasts only about five seconds, that the partition is secreted. The partition is at first shaped like a washer, having a large hole in the center. The hole results from the absence of glands along the front median margin of the head. This area of the head is located in the center of the partition during the rotating movement and at the end of the rotation protrudes through the partition opening (Fig. 3, B).

Following the initial secretion of the partition, the head is flexed and the worm moves the glandular surface back and forth over the partition. This final action apparently reinforces the partition and probably accounts for the reduction

of the original opening to two to four small perforations. It is difficult to understand why the original opening would not be completely sealed over.

As additions are made to the lower part of the tube, the tube partitions are continually removed and replaced at lower levels. In removing a partition the worm moves head downward to the site of the partition. The body is flexed at the level of the fourth parapodia and then twisted slightly at the level of flexure so that the right side of the body is closer to the periphery of the partition than is the left. The large, heavy, blade-like 4th seta is now extended downward and then retracted. With each downward stroke, the truncate blade of the seta cuts through the partition where it joins the tube wall (Fig. 3, C). Between each cut the body rotates slightly counterclockwise, and the seta performs another cutting stroke. When the worm makes a full circle, the partition is completely severed from the tube wall. The partition is now pushed down and back against the inner surface of the tube wall, where it is gradually plastered to the wall as additional secretions are laid down. Such old partitions can be observed along the length of the lower part of the tube, but as the tube wall becomes thicker and darker, the incorporated partitions become invisible.

The left 4th seta was never observed being used for cutting a partition. However, in view of the fact that the left seta is as highly developed as the right, it is likely that either seta can be employed in cutting partitions.

In addition to removing tube partitions, the enlarged blade-like 4th setae are also used to slit open the side of the tube to permit the formation of an entire new extent of tube. In initiating such a new construction, the worm makes an irregular transverse cut through the tube wall. The anterior body region is pushed through the rupture and begins the laying down of new tube as already described. The old lower section of the tube is no longer used, and the entrance to it is gradually sealed off.

Such a major alteration was observed only at the lower part of the tube. Whether an entire new tube could be rebuilt in this manner is not known. However, when specimens with obvious new side branches to the tube were found in the field, the new branch was always located in the lower part of the tube.

Observations on tube construction were not limited to the building of additions to an existing section of the tube. Worms observed in capillary tubes would secrete normal additions to either end of the glass tubing, particularly the lower end. Partitions were also constructed and removed within the capillary tubes.

In contrast to *Chaetopterus*, *Spiochaetopterus* is capable of burrowing and rebuilding its tube when removed from the original one. Specimens were removed from their tubes and placed on the surface of a mud-sand substratum within a small beaker. The worms immediately began to burrow downward head first and very shortly disappeared below the surface. Within an hour palps were visible projecting from the mouth of an opening at the surface of the substratum. When excavated, a delicate short tube was uncovered.

Feeding

Most of the observations on the feeding mechanism of *Spiochaetopterus* were made on worms placed in capillary tubes and fed a suspension of carmine particles in sea water or a suspension of stained Pabulum.

Spiochaetopterus, like many sedentary polychaetes, is a ciliary feeder. It has been suggested that the grooved ciliated palps might be the principal structures used for obtaining food. This was not found to be true. The palps are primarily used for removing waste and other unwanted materials from the tube and only secondarily as organs of ingestion.

The feeding mechanism is basically like that of *Chaetopterus* (MacGinitie, 1939), in that a water current is passed through a mucous bag, straining out suspended particles, but the process differs from that in *Chaetopterus* in a number of important respects. As described earlier, the middle region of the body of *Spiochaetopterus* bears very distinctive parapodia (Fig. 1, C), each composed of a foliaceous notopodium and an uncinete neuropodium. The foliaceous notopodium is composed of a dorsal and a ventral division. The larger dorsal division bears two lobes, one of which is curved toward the mid-dorsal line; the other is curved ventrally. When held erect, *i.e.*, at right angles to the body axis, the divisions and lobes of the two notopodia so appose each other that they form three ring-like openings, one mid-dorsal and two dorso-lateral (Fig. 4). The mid-dorsal ring is formed by the two incurved lobes from each dorsal division. Each lateral ring is formed by the ventral division and the ventrally curved lobe of the dorsal division.

The inner margins of the rings are lined by large membranelles, which are visible even at a magnification of $30\times$. The effective stroke of each membranelle is directed posteriorly but does not occur in all membranelles of a ring simultaneously. Rather, the beat occurs as a sequence of several waves, which progress around the ring in a clockwise direction.

The beating of the membranelles within the notopodial rings drives water through the tube. The notopodia of the middle body region are held outstretched at right angles to the body axis, and their outer margins touch the tube wall. The ventral body surface with its short uncinete neuropodia is in contact with the opposite wall of the tube. Thus, all water must pass through the ciliary notopodial rings. At the level of any one parapodium there would be three currents, one dorsal and two dorso-lateral, corresponding to the three notopodial rings (Fig. 4).

A mid-dorsal ciliated groove traverses all three regions of the body and terminates just behind the mouth. The groove in the middle region of the body thus crosses the inner wall of the mid-dorsal ring. Behind each ring the groove widens to form a ciliated cupule, except for the first segment of this body region, which lacks a cupule. Anteriorly the cupules are large, well-developed, and located some distance back from the preceding ring. Posteriorly they become progressively less conspicuous and located closer behind the preceding mid-dorsal notopodial ring.

The water current passing through the tube contains suspended detritus and plankton upon which the worm feeds. Although the water current, which thus functions as a feeding current, is created by all of the notopodial rings, the mid-dorsal ring is more directly involved in feeding. Each of these mid-dorsal rings (at least anteriorly) secretes a mucous bag, the end of which is caught and rolled up as a food ball by the cupule located behind the ring (Fig. 4). New mucous film is continuously being produced by the notopodial ring during the feeding process. All of the water passing through a mid-dorsal ciliary ring must also

pass through the mucous bag secreted by that ring. The food particles strained out and collected in passage are consolidated as a food ball as the bag is rolled up by the cupule.

Active feeding, *i.e.*, the secretion of mucous bags, is more or less simultaneous and appears to be limited to the anterior segments of the middle body region. The greatest number of mucous bags and food balls ever observed at one time was thirteen. The food balls formed more posteriorly are considerably smaller than those formed by the first few anterior segments.

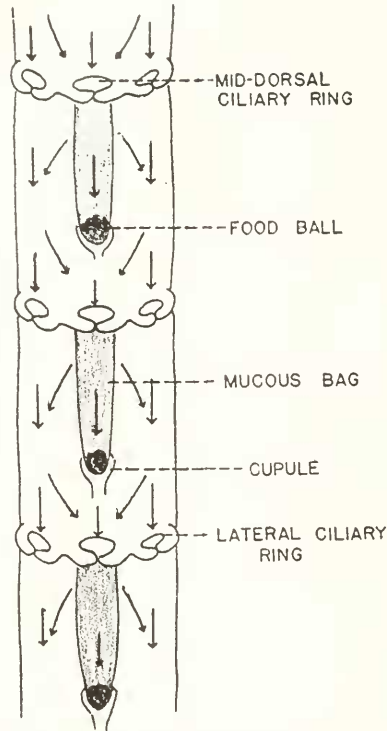


FIGURE 4. Dorsal view of three segments of middle body region showing the position of mucous bags and the formation of food balls. Arrows indicate the direction of water currents.

When a food ball of adequate size has been attained, secretion of mucous film is halted, and the bag is detached from the notopodial ring and completely rolled up by the cupule. The food ball is then carried forward along the mid-dorsal ciliary groove. On reaching an anterior cupule the food ball may be added to the food ball being formed there, or more frequently, the forward moving food ball forces the evacuation of the food ball in that cupule. The food balls thus tend to be carried anteriorly as an irregular string. When the food ball passes through a ciliary ring, which, it will be remembered, is driving water in the opposite direction, the two notopodia separate slightly and are inclined somewhat anteriorly.

As soon as the food ball passes, the notopodia return to their normal position. The entire cycle of movement takes place within a second or less. The membranelles were never observed to cease beating nor to reverse their beat.

Eventually the food balls reach the anterior end of the dorsal groove, which terminates just in front of the convex lower lip flanking the posterior side of the mouth (Fig. 1, B). They are then driven by the general surface ciliation over the lip into the mouth.

The time required for complete formation of a food ball was not measured. When worms were fed a suspension of carmine particles or stained Pablum, food balls were formed and passed anteriorly in less than a minute. But this is certainly far more rapid than would occur under natural conditions where detritus is fine and less concentrated.

The presence of a food bag tends to change the pressure of the water current passing through the dorsal ciliary ring as compared to the lateral rings. This results in the production of compensating currents crossing between the three main streams (Fig. 4). Thus, some of the water passing through the lateral rings at one level passes over and enters the middle ring at the next segment, bringing with it a new source of detritus to be removed by the food bag at this level. Eventually, almost all of the water passing posteriorly through the tube is strained through a mucous bag. This apparently occurs by the level of the first twelve or so segments and would account for the decreasing size of the food balls and absence of mucous bag formation more posteriorly.

Although feeding most commonly occurs with the head directed upward within the tube, worms were observed on occasion to feed while in a head downward position.

The principal function of the palps, as will be described later, is egestion and maintenance of an unobstructed tube. But the palps were occasionally observed to act as secondary or accessory feeding organs. Small masses of detritus were carried down the palps and into the mouth within the large ciliated gutter of the palp.

Water circulation and egestion

Much of the body of *Spiochaetopterus* is clothed in fine cilia, but it is the membranelles of the notopodial rings that create the water current upon which the life of the worm depends. The membranelles were never observed to cease beating nor were they ever observed to reverse their beat. Their beating creates a continual water current passing through the tube. Although feeding is restricted to the first twelve or so notopodial rings, all of the notopodial rings are involved in the production of the water current. When the worm is directed upward, the current enters the mouth of the tube at the surface of the substratum; when the worm is directed downward, the current enters the buried lower end of the tube, seeping in from the surrounding mud and sand.

The continual passage of water through the tube functions not only as a feeding current, as has already been described, but also as a respiratory current and a current for the removal of waste. *Spiochaetopterus* is devoid of gills, as might be expected in an animal of such small size. Respiratory exchange occurs across the general body surface.

The long delicate palps of *Spiochactopterus* are highly effective organs for the removal of egested waste and any over-large masses of detritus brought in by the water current. Each palp is provided with a small ciliated groove which runs just lateral to the broad, deep, gutter. Cilia within the groove beat anteriorly toward the palp tip, *i.e.*, in the opposite direction from that of the water current produced by the membranelles. Any large object or large mass of detritus carried into the tube by the water current becomes entangled in mucus produced by the palps. The undesired material is then carried anteriorly along the ciliated groove of one of the palps. If the worm is below the upper end of the tube, as is often the case, it moves upward in the tube until the tips of the palps project from the tube opening. The detritus mass being carried along the palpal gutter is now ejected from the tip of the palp and falls to the surface of the surrounding substratum.

The efficiency of the palps in preventing clogging of the tube was especially evident in feeding experiments using a suspension of carmine particles or dyed Pablum. When a drop of suspension was released at the opening of the tube, a large amount of the material was immediately drawn into the tube. However, as soon as the suspended material reached the level of the palps, the larger particles were quickly collected by these structures and moved on the palpal groove back toward the exterior. The worm rapidly moves upward in the tube during this process. Only the finest of the suspended particles passes by the palps and is collected by the mucous bags.

The palps also function in the removal of feces. Egested wastes are released from the anus as elongated fecal pellets, shaped like a grain of rice and about twice the size of a food ball. On leaving the anus the pellets are picked up by the ciliated mid-dorsal groove, which runs the entire length of the body, beginning just in front of the anal opening. This is the same groove which transports the food balls, and in the mid-region of the body the fecal pellets pass through the notopodial ciliary rings in the same manner as a food ball. On reaching the anterior end of the dorsal groove, the pellets are transferred to the palpal groove for ejection to the exterior. With every release of a fecal pellet by the anus, and several may be released at one time, the worm moves toward the top of the tube to permit the palps to eject the pellets from the tube opening. How fecal pellets are differentiated from food balls is not clear, for only occasionally is a fecal pellet ingested. Perhaps the difference in shape or size is a factor.

Patterns of activity

Worms placed in capillary tubes could be kept in good condition and observed for weeks. The easy adjustment of these animals to glass tubes made it possible to observe in some detail the activity patterns of their tubicolous existence. The only limitation to these observations was the fatigue of the observer who had to constantly watch the worms both with the unaided eye and through a dissecting microscope. From a number of such observations, two seven-hour records (Fig. 5) are presented as being fairly representative. The data provided by these observations should in large part be applicable to worms living under normal conditions in natural tubes.

A number of facts regarding the activity patterns of *Spiochactopterus* are indicated by these records. The worms are by no means stationary inhabitants of

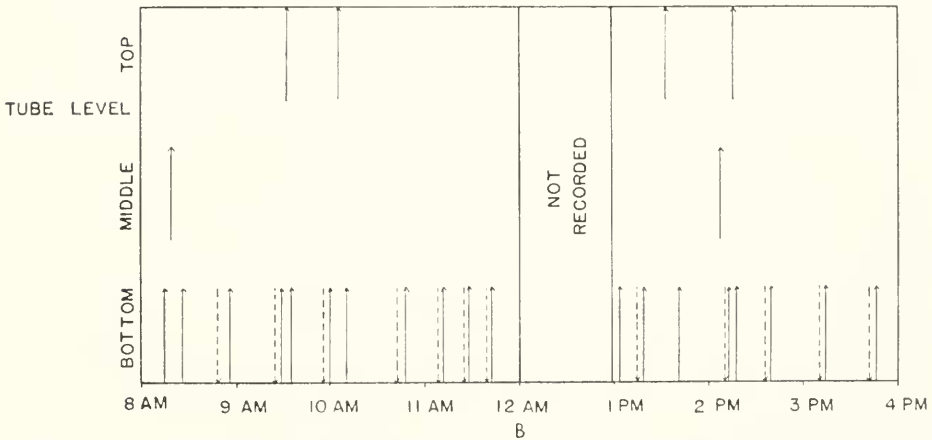
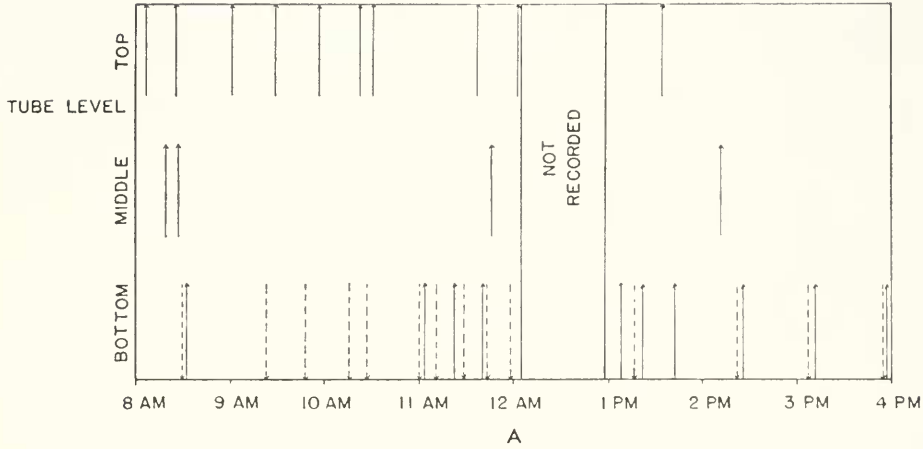


FIGURE 5. Records of the activity patterns of two different worms over a seven-hour period. Each arrow represents a position assumed by the worm and the time that the position was first assumed. The interval of time spent in that position is indicated by the space between two arrows. Solid arrows represent a head-upward position; dashed arrows represent a head-downward position. The three vertical levels represent levels occupied by the worm within the tube. Worm A spent a total of 66% of the time recorded at the bottom of the tube. Worm B spent over 90% of the time recorded at the bottom of the tube.

their tubes, but continually shift position within the tube. As many as eight or nine changes in position occur within an hour. Yet the pattern of movement is very irregular; it is not cyclic nor predictable.

Although a worm frequently inverts itself and is capable of remaining upside down for a long period of time, it most frequently assumes an upright position. This is not surprising in view of the structure of the tube, the means by which a water current is produced, and the mechanism of feeding and egestion. Inversion

strongly associated with the feeding activity of the worms out of the tube. In all 16 mounts the attraction is toward the sides (Figure 1).

Feeding is the usual activity when the worms are stationary, and the worm can rest its head on any level within the tube. However, this activity is more commonly observed out in the flume, in the yard. All worms observed about the ground part of the tube hung at the bottom of the tube. All came to the top a number of times during the observations period, but always always this was to remove mucus or clear the tube. The worms would then return to the bottom.

Although there were no occasions in similar tubes, for this would probably fail the feeding behavior of these worms with exposed tubes. The small diameter of the tube provides surface—bottom contact at each even movement of the tube above the water table. Mucus is a major factor in the structure of worms would be expected.

DISCUSSION

Streblospio and *Chironomus* have been distinguished as a pair of species with regard to swimming and tube building activity. Many of these differences appear to represent adaptations to different types of tubes. The genus *Chironomus* constructs the largest tubes of the family and the tube has a diameter of several centimeters. The soil in this tube contains a large volume of water passing through it. A stream of water of large size is moved efficiently by many bundles of *Streblospio* swimming. Neither tube building nor water is done through the tube of *Chironomus* in the laboratory setting. A water column of the size of this tube could not be built by the *Streblospio* in the lab.

In *Chironomus*, a single-muscle feeding leg is produced by the long wing-like 12th abdominal segment which is part of the middle body region. In *Streblospio*, the 12th abdominal segment is divided by the numerous setae of the middle body region and is made up of 15 legs and produces simultaneous. At least the latter part of the abdomen, beginning the 11th abdominal segment (Hynes 1971), assists in the swimming and all segments of the abdomen appear to work the same manner as *Streblospio* does.

The principal passage of a large volume of water into the tube and out the other end of the tube is done by *Chironomus* when the tube is flushed out of feet and legs. *Streblospio* is too large to be used as feet. When such large swimming devices are located in the head region, the compressed 12th abdominal segment is on the dorsal surface of the side of the leg. Thus in *Chironomus* and similar tube swimming devices must be drawn back on the alternate of the tube.

The structure of the difference in *Streblospio*—there is only a slight surface opening to the tube with the opening well below the entrance of the head. *Chironomus* has a large opening at the top. Since the water column passing through the tube is a smooth stream moving through the middle legs the feeding legs must be kept clear of large obstructing particles or debris. In addition, soft foreign material and feces must be cleared out of the tube opening region, and moving water column. Swapping out the elasticity of any material in the anterior portion of the tube of *Streblospio* or the middle and greater abdominal segments in those of *Chironomus*.

Streblospio is a tube swimmer. In the *Chironomus* the tube is used as a swimming tube. *Streblospio* is a tube swimmer. The tube of the *Streblospio*

Telepneustes, *Phyllochlaetopterus* and *Mesochlaetopterus*—all possess long gills, and significantly all possess at least one or two rough tubes with the cover end buried in the substrate. Only *Chlaetopterus* has short pairs and only members of this genus construct U-shaped tubes with separate surface openings for the entrance and exit of the water current. It is probable that the presence of long pairs in *Chlaetopterus* is a secondary condition.

The comparison of the tube structure in *Chlaetopterus*, *Mesochlaetopterus*, and *Manzanilloa*, and in comparison with the tube of *Telepneustes*, *Phyllochlaetopterus* and *Telepneustes* (Fernald, 1927). However, in both *Chlaetopterus* and *Spinichlaetopterus* the gills for the secretion of the tube are located on the ventral side of the anterior portion of the body and the presence of lesser or equal to a somewhat similar manner. This is very likely one of the chief members of the family as well.

All of the *Chlaetoptera* possess the enlarged, highly modified, tubular setae described for *Telepneustes* and as in *Spinichlaetopterus* it is probable that these setae form or in all members of the family, but not on the side of the tube wall. Fernald (1927) described the opening of the side of the tube by *Chlaetopterus* but did not explain the mechanism. It is very likely that the function is performed by the 4th setae.

Continuation of some of these observations regarding the building and feeding from a study of other members of this very unique family of polychaetes. The author hopes to undertake this task in the near future.

DISCUSSION

1. *Spinichlaetopterus* constructs a small, circular, associated tube approximately 0.75 mm in diameter and eight or more centimeters in length. The tube is constructed vertically to horizontal or vertical and has only a few millimeters of the upper end of the tube projecting above the surface of the substrate.

2. The tube is secreted by epidermal glands extending along the entire external ventral surface of the anterior body region.

3. One vertical cylindrical column is secreted at a time, the length of the cylinder corresponding to a segment between annulations. The wall is gradually thickened with additional secretions.

4. Temporary transverse internal tube partitions are constructed in the lower part of the tube. The partitions are perforated by several openings.

5. An entire new lower region of tube may be constructed at a branch of the old tube. The lower part of the old tube is then sealed off.

6. In constructing such a branch, the old tube wall is not torn, and one of a pair of greatly enlarged tubular setae of the former segment. These setae are assumed to remove the temporary tube partitions.

7. The water current through the tube is produced by the beating of parapodia which line three ring-like openings formed by the filaments, secondary of each segment in the middle region of the body.

8. The mucronal ring of each of the first 15 or 16 filaments, parapodia secrete a mucous bag which means up the tentacles and placodes from the water current passing through the tube. The mucous bag is tough and rolled up as a

food ball by a cupule located behind each ring. The food ball is then passed forward to the mouth along a ciliated mid-dorsal groove which runs anteriorly from the posterior tip of the body.

9. The greatly elongated palps function chiefly to remove feces and also to remove over-large masses of detritus which enter the tube with the water current.

LITERATURE CITED

- ENDERS, H. E., 1908. Observations on the formation and enlargement of the tubes of the marine annelid, *Chaetopterus variopedatus*. *Proc. Indiana Acad. Sci.*, **1907**: 128-135.
- ENDERS, H. E., 1909. A study of the life history and habits of *Chaetopterus variopedatus*. *J. Morph.*, **20**: 479-532.
- FAUVEL, P., 1927. Polychètes sédentaires. *Faune de France*, **16**: 1-494.
- MACGINITIE, G. E., 1939. The method of feeding of *Chaetopterus*. *Biol. Bull.*, **77**: 115-118.
- MACGINITIE, G. E., AND N. MACGINITIE, 1949. *Natural History of Marine Animals*. Pp. 1-473. McGraw-Hill Book Co., Inc., New York.